

On the Classification of the Reptilia.

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It is gradually becoming recognised that the class Reptilia is not a monophyletic group of diverging forms sprung from a common stem, like the class Aves or the class Mammalia; but is an assemblage containing, on the one hand, the ancestors of the Mammalia, and, on the other hand, the ancestors of the Birds, together with the early Amphibian-like Amniotes, which became adapted to a terrestrial mode of life. In fact, the Reptilia represent not a class but a grade of structure. This group includes a main stem leading from the Stegocephalian type to a central point of divergence of two main branches, one giving rise to the Birds, the other to the Mammals (as shown in the diagram, fig. 1). In addition, there are, of

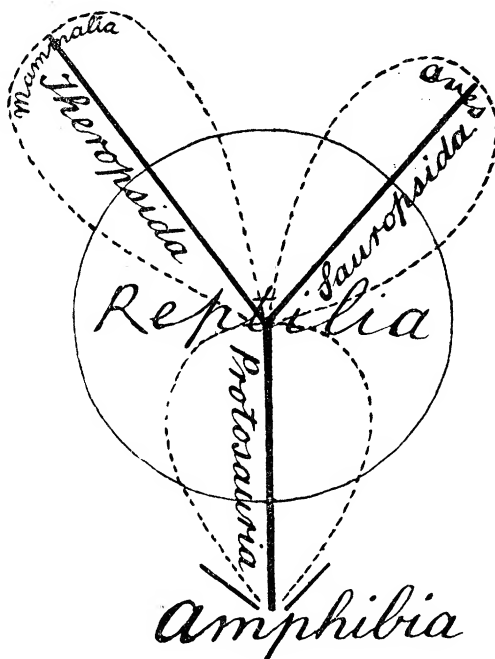


FIG. 1.

course, many abortive side twigs. Some day, no doubt, when the exact relationship of the various living and extinct reptiles has been more accurately determined, it will be necessary to split up the artificial group Reptilia, assigning some to the Mammalia and some to the Aves; but for the

present we may be content with keeping the class Reptilia, always remembering that it is a grade of ill-defined limits.

The modern views of the phylogenetic relationships of the various orders of Reptilia may be said to have arisen chiefly from the work of Cope and Baur, following on the conclusions of Huxley and other earlier authors. To the ingenuity of Cope we owe the valuable suggestion that the starting-point of the divergence between the Amphibia and the Reptilia was determined by the structure of the vertebral column—the vertebral body being mainly derived from the hypocentrum in the former and from the pleurocentrum in the Amniota. Being thus provided with a means of distinguishing the early reptiles from their Amphibian relatives, the next step is to seek for characters enabling us to trace out the diverging lines among the Reptilia themselves. Here again we are indebted to Cope (13), but more especially to Baur (1, 2) for pointing out the importance of the roofing of the skull in classification. Whereas the earliest and most primitive reptiles have, like their Amphibian ancestors, a roofing complete over the temporal region, this becomes pierced in others by one or two foramina. Thus are left one or two longitudinal temporal arches. The formation of the foramina or fossæ is generally accompanied by a reduction in the number of bones covering the hinder region of the skull. It is not my intention to enter into a detailed account of these points in this paper; they have been discussed by many authors, and are well understood. It will be sufficient for our present purpose to point out how profoundly the modern classification of the Amniota has been affected by their recognition.

Owen and Cope long ago drew attention to the Mammalian affinities of certain fossil reptiles now included in the orders Cotylosauria and Theromorpha; while Huxley emphasised the relationship of the birds to the other orders, more especially the Crocodilia and the Dinosauria. Huxley, indeed, included the Reptilia with the Aves in the group Sauropsida, and believed the Mammalia to have been independently derived from more Amphibian-like ancestors. He failed at that time (17) to appreciate the fact that his group Sauropsida included forms, like the Dicynodontia and the Sauropterygia, which belong in all probability to the Mammalian line.

When, chiefly owing to the remarkable discoveries of Seeley and Broom, the true affinities of the extinct Theromorpha became established, the tendency to split the Reptilia into two diverging branches became more pronounced. The importance of the skull-roofing in this connection was appreciated by A. Smith Woodward (37), but it was not till 1903 that Osborn definitely attempted to divide the whole class Reptilia into two

groups which he called the Synapsida (with one lateral temporal fossa and one bar) and the Diapsida (with two lateral temporal fossæ and two bars). This paper marks an epoch in classification. In the Synapsida were placed the Cotylosauria, Anomodontia, Testudinata, and Sauropterygia; in the Diapsida were placed the Protorosauria, Pelycosauria, Rhynchocephalia, Procolophonia, Proganosauria, Choristodera (Simædosauria), Rhynchosauria, Phytosauria, Ichthyosauria, Crocodilia, Dinosauria, Squamata, and Pterosauria. But, owing to a great extent to the incomplete state of knowledge at the time, this classification has many weak points and requires modification. For instance, it is now generally recognised that the Cotylosauria (and allied Pareiasauria, Procolophonia, and Microsauria) belong to a low grade of reptiles preserving the original complete roof of the skull, and other Stegocephalian characters. Among these primitive forms will perhaps some day be distinguished the ancestors of the more advanced Synapsida and Diapsida; but, for the present, they may be included in a provisional assemblage of early reptiles forming a sub-grade rather than a true sub-order. In the second place, various orders are placed in Osborn's Diapsida which on further evidence seem to belong to the Synapsida—such as the Pelycosauria, Proganosauria, and possibly the Ichthyosauria.

Useful and important as the roofing of the skull is in classification, it is often difficult if not impossible to ascertain for certain its structure in fossils. Moreover, as is always the case when we endeavour to classify by a single character, we are liable to confuse forms in which foramina have begun to appear with others in which they have been or are being secondarily obliterated, and to misinterpret aberrant modifications. Consequently many reptiles have been repeatedly shifted backwards and forwards from the Diapsida to the Synapsida. Any corroborative evidence derived from other parts would therefore be of value as a clue to affinity, and it is the object of this paper to show that such evidence may be found in the structure of the heart and of the skeleton of the hind foot. The former unfortunately only applies to living forms; but the latter is often available even in fragmentary fossils.

For the purpose of facilitating description, and of making our results clear, the grade or class Reptilia may be provisionally subdivided into three groups (fig. 1):—In the first, which may be called the Protosaurian group, we place the primitive forms connected with the Amphibia and leading on from them to the central point of divergence of the Synapsida and Diapsida, together with other side branches. The Protosauria, then, include the Microsauria, Cotylosauria, Pareiasauria, and Procolophonia (see p. 269). The second group, in which becomes developed one lateral temporal foramen

limited below by a single bar, includes those reptiles which lead towards the mammals, together with side branches. These synapsidan reptiles and the Mammalia make up a monophyletic offshoot to which the name Theropsidan branch may be applied. Lastly, the majority of the reptilian orders belong to the third group, culminating in the Aves, and in which two lateral temporal foramina and two bars are developed. These are the Diapsidan reptiles, and together with the Aves they form the great Sauropsidan group. This attempt at a phylogenetic classification of the Amniota may be expressed in diagrammatic form as shown in fig. 1. In these general conclusions most zoologists would now concur; it is only when we try to assign certain families and orders to definite positions in the system that serious differences of opinion arise. We can now pass to the evidence on which these conclusions are founded.

The Significance of the Metatarsals in Reptilian Phylogeny.

On examining the skeleton of the hind foot of a typical Lacertilian, such as the Iguana shown in fig. 2, C, it is at once seen that, whereas the first four metatarsals are of the normal elongated and straight shape, the fifth metatarsal is quite peculiar, and differs from the others in that it is shortened and markedly hooked. The bent proximal end projects forwards (inwards), and also extends farther proximally than the remaining metatarsals, passing over the end of the fourth. This peculiar shape and disposition of the fifth metatarsal has, of course, been often noticed by anatomists, but its significance in classification seems not to have been fully appreciated. Much controversy has taken place about the exact homology of the hook-shaped bone. Some believe it to represent the modified fifth distal tarsal, others the fifth metatarsal combined with its tarsal, and yet others that it represents the modified fifth metatarsal only. This last interpretation is the one now generally accepted, and is clearly shown in Sewertzoff's excellent account (31) of the development of *Ascalobotes* (see fig. 2, D, E). The question of its homology scarcely concerns us here; the important point to establish for the purpose of this paper is that this peculiarity is found in the hind foot not only of all known Lacertilia, but also of all living reptiles. So far as I can ascertain, it occurs in all Chelonia, Rhynchocephalia, Crocodilia, and Lacertilia, excepting, of course, in those forms which have lost the hind limb. Examples are shown in fig. 2. This particular specialisation of the fifth metatarsal is therefore far more constant than the structure of the skull. Once acquired it never seems to be lost, and it can still be clearly seen even in the feet of the Chelonidæ or the Pythonomorpha, which have become so highly modified into swimming paddles. The hook-shaped metatarsal does

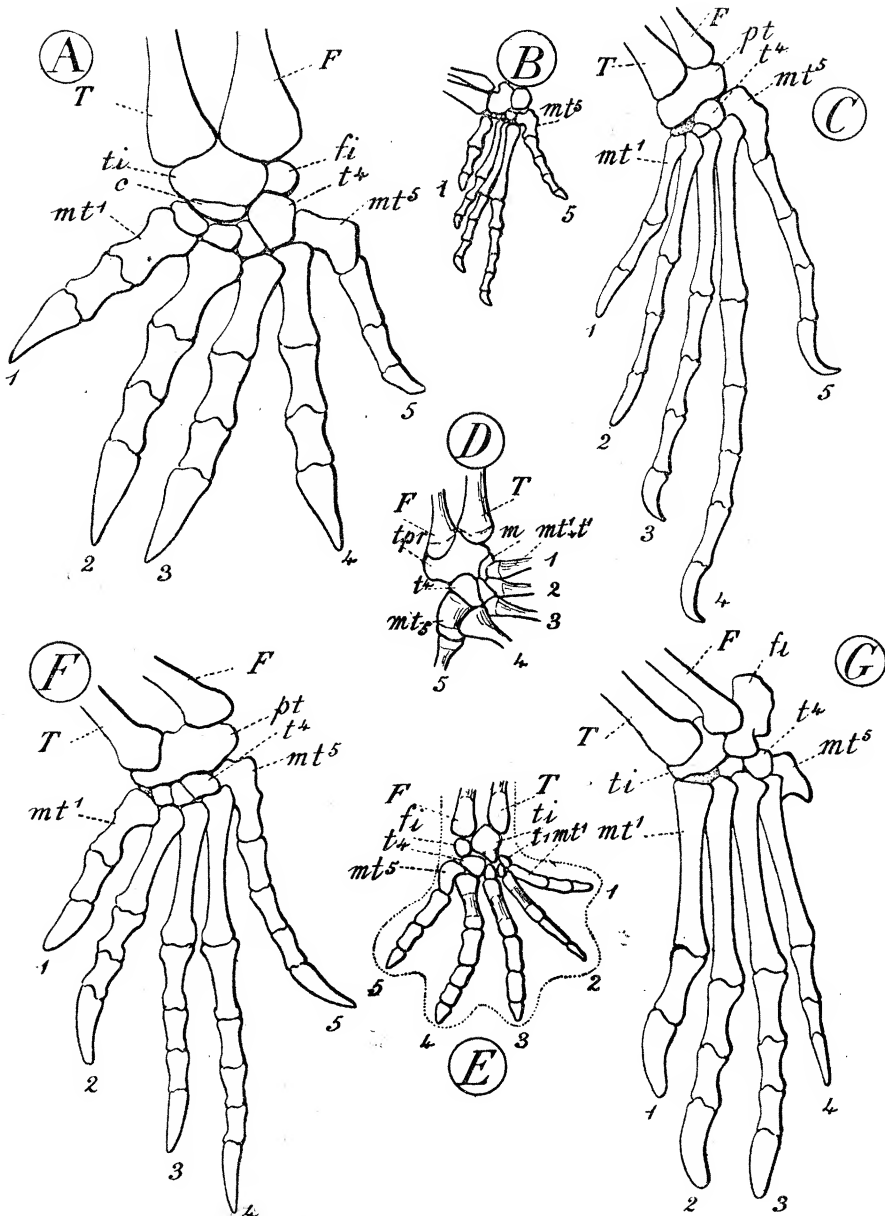


FIG. 2.—Skeleton of the Hind Foot of:—A, *Chelydra serpentina*, L.; B, *Sauranodon* (*Sapheosaurus*) *incisivus*, Jourdan; C, *Iguana tuberculata*, Laur.; D, *Ascalobotes fascicularis*; E, Embryo of same species; F, *Sphenodon punctatus*, Gray; G, *Caiman sclerops*, Schn. D and E copied from Sewertzoff (31), B from Lortet (21), A, C, F, G, from photographs of specimens in the Oxford University Museum.

not seem to be closely related to any particular mode of life or method of progression, being essentially the same in reptiles of the most diverse habits. Its development is possibly correlated with the formation of the mesotarsal articulation so characteristic of the Sauropsidan reptiles and birds. It is also accompanied by the disappearance of the fifth distal tarsal. Since there is no reason whatever to suppose that it has arisen independently in the various orders, we can only assume that the hook-shaped metatarsal was present in the common ancestor of all the forms which possess it. The mesotarsal articulation, above referred to, is due to the close connection or fusion of the proximal tarsals with the tibia and fibula, and the distal tarsals with the metatarsals.

Now, in the Mammalia, the fifth metatarsal is of normal structure. When the fifth digit is not reduced its metatarsal is straight, and articulates with the cuboid (fourth and fifth distal tarsals fused) at the usual level. We should not therefore expect to find a hook-shaped metatarsal in any fossil reptile leading towards the Mammalia, and this expectation is fulfilled, since there is no trace of it in the Theromorpha.

Of the remaining Reptilia with one fossa and bar, the Ichthyosauria unfortunately yield no certain evidence, since their foot is too modified. But the more primitive Sauropterygia, such as the Lariosauridæ, clearly display a normal fifth metatarsal (fig. 3, F), thus confirming the view, which is now gaining ground and based on other evidence, that the Sauropterygia are allied to the Theromorpha. This view is, of course, incompatible with that of Jaekel, who believes the Sauropterygia to be Diapsida which have lost the lower temporal bar.*

Also, if our contention is correct, that the modified fifth metatarsal is a specialisation occurring only in that line of reptilian phylogeny leading towards the Birds, we should expect to find it absent in all the Cotylosauria and allied Protosaurian forms. Here, again, the facts support our view, for these early reptiles have normal metatarsals like their Amphibian ancestors.

It is clear, then, that we have here a valuable corroborative character to help us to decide whether a given species belongs to the Theropsidan or the Sauropsidan line of evolution. It will not be necessary in this paper to give a description of the metatarsus of all known living and extinct Reptiles; the results of my investigations, based as far as possible on the examination of actual specimens, but also to a great extent on the published figures and descriptions of others, are summarised on page 274. But it is interesting to consider briefly certain important genera and larger groups whose position

* 'Zool. Anz.,' vol. 35, 1909.

has hitherto been very uncertain, and in which the structure of the skull fails to yield decisive evidence.

Mesosauria (Proganosauria).—The very ancient fossils, *Mesosaurus tenuidens*, Gervais, from South Africa, and the closely allied *Stereosternum tumidum*, Cope, from South America, were placed in a new order Proganosauria by Baur (1), who believed them to be related to the Rhynchocephalia. Osborn

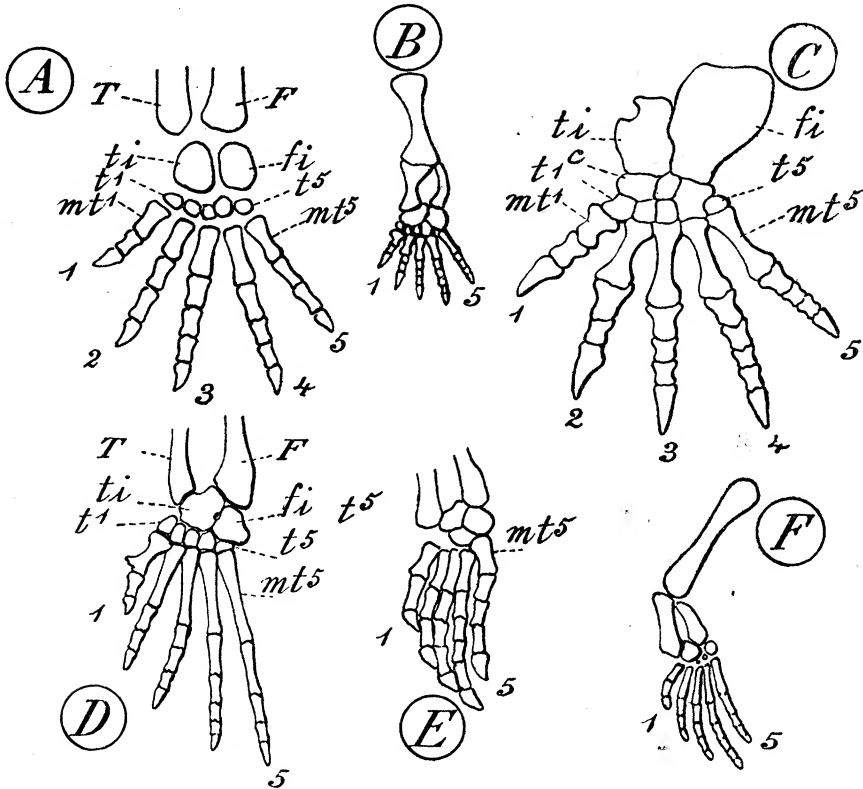


FIG. 3.—Skeleton of the Hind Foot of :—A, *Palæohatteria longicaudata*, Cr., from Credner (14); B, *Procolophon*, from Watson (33); C, *Naosaurus*, from Osborn (27); D, *Mesosaurus* (*Stereosternum*), from a specimen in the British Museum; E, *Pleurosaurus goldfussi*, H. v. M., from Lortet (21); F, *Lariosaurus*, from Boulenger (6). All, except E, are somewhat restored.

included them in the Diapsida (26); and in a more recent paper, McGregor, (23), on what appear to be very insufficient grounds, claimed that *Mesosaurus* has a skull with two temporal fossæ, and is allied to the Rhynchocephalia and Protorosauria (including *Palæohatteria*). He denies the affinity with the Plesiosauria upheld by Seeley (29), and afterwards so well supported by Boulenger (6). Williston refuses to commit himself (34), but inclines to the view that the Mesosauria are allied to the Theromorpha.

or possibly independently derived from some Cotylosaurian. Broom's observations on the South African fossils (8) seem to lead him to the opinion that they belong to the Diapsida, but yet possessed only one temporal fossa, while von Huene insists on the presence of one fossa only. An examination of the excellently preserved specimen of *Stereosternum* in the British Museum (fig. 3, D) shows us at once that it cannot be closely allied to the *Rhynchocephalia* or any known *Sauropsidan*. Not only is it remarkable in the possession of five distinct distal tarsals, but also in the absence of a mesotarsal articulation, and in that the fifth metatarsal is the longest of all and of quite normal shape. Since we know that the primitive *Sauropterygia*, such as *Lariosaurus*, had a normal fifth metatarsal, the view of Seeley and Boulenger seems to be by far the best established.

Palæohatteria.—The history of this genus is instructive. First described by Credner (14) under the impression that it is closely related to *Sphenodon*, it was credited with a skull provided with two lateral temporal foramina, and for long figured in text-books and other writings as a typical *Rhynchocephalian*. Baur placed *Palæohatteria* in his order *Proganosauria* (3), including it in the *Protorosauridæ*, which he placed with the *Mesosauridæ* and *Champsosauridæ* in the *Proganosauria* as a sub-order of the *Rhynchocephalia*. Subsequently Williston (34) dwelt on the affinity of *Palæohatteria* with the *Theromorphs*, threw doubt on Credner's reconstruction of the skull, but included this genus together with *Protorosaurus* in one sub-order *Protorosauria*. In a later paper (36) Williston gave further arguments for his view, and strongly urged that there is no evidence that either in *Palæohatteria* or in *Protorosaurus* there was more than one pair of temporal fossæ, thus agreeing with von Huene.

The hind foot of *Palæohatteria* (fig. 3, A), provided with a normal elongated fifth metatarsal, shows clearly that it cannot belong to the *Rhynchocephalia*; rather should it be classified in the *Saurotherian* group with other reptiles having a single temporal fossa.

Protorosauria.—The important genus *Protorosaurus*, first described as a crocodile by Spener in 1710, was placed by Seeley in a special order of doubtful affinity but not far from the *Dinosauria* (28). Unfortunately the skull is not thoroughly known, and it has not yet been determined whether both superior and inferior temporal foramina were present. Long ago, however, it was shown by von Meyer (24) that the hind foot of *Protorosaurus* is provided with the characteristic *Sauropsidan* hook-shaped metatarsal, so that we may take it as established that this genus, about whose systematic position there has been so much speculation, is related to the primitive *Rhynchocephalia*, *Crocodylia*, or *Dinosauria*, and has no connection with the *Mesosauria*.

Related also to these Sauropsidan reptiles would appear to be the Aetosauria or Pseudosuchia (v. Huene, 16), the Parasuchia (McGregor, 22), the Simcedosauria (Lemoine, 20; Brown, 10), and the Rhynchosauria (Huxley, 18), since they all have upper and lower temporal foramina and a hook-shaped fifth metatarsal. On the other hand, the Procolophonia, believed by Broom to have Rhynchocephalian affinities, and placed by Osborn in the Diapsida (26), are now known to have neither temporal fossæ nor a modified metatarsal. For the present they may be placed in our Protosaurian group, and are probably related to the Paraiasauria and Cotylosauria as maintained by Boulenger (7) and Seeley (30).

Pelycosauria.—Founded by Cope in 1878 for certain North American fossil reptiles, such as Dimetrodon and Clepsydrops, supposed to be allied to the Rhynchocephalia, the systematic position of this order has been a subject of much controversy. Cope soon changed his mind and, struck by the resemblance of the Pelycosauria to the South African Theromorpha, believed them to have mammalian affinities. In 1897, however, Baur and Case (4) thought they had proved the existence of upper and lower temporal fossæ, and later the Pelycosauria were included in the Diapsida by Osborn (26). Subsequently Case in his valuable revision of the Pelycosauria (11) still insisted on their close relationship with the Rhynchocephalia, Proganosauria, and Protorosauria. Now the Proganosauria (Mesosaurus and Palæohatteria) we have already seen are probably not Diapsidan, and Broom has recently brought forward strong evidence that the skull of the Pelycosauria is really built on the Synapsidan plan (9). Cope's later opinion is thus borne out, and is certainly more in agreement with the fact that the foot has five normal metatarsals, as described and figured by Case (11) and Osborn (27), see fig. 3, C.

Aræoscelis.—Under the name *Aræoscelis* Williston has recently described (35) an interesting Permian reptile of lizard-like shape. It is provided with single upper lateral temporal foramen and a broad arch below. These and other characters lead him to suppose that the Lacertilian skull has been evolved from some such form by the narrowing of the arch and the loosening of the quadrate. But if the figure given of the hind foot (36, fig. 5K), and the restoration (36, fig. 7) correctly represent the fifth metatarsal as an elongated straight bone, there can be little doubt that *Aræoscelis* is not closely related to any modern reptilian order. Rather would it seem to belong to the Theropsida; unless perchance it is an early representative of the Sauropsida before the metatarsal had become modified.

Pleurosauros.—Watson, who has recently redescribed the skull of *Pleurosauros goldfussi*, V. Meyer (33A), supports Boulenger's contention (5) that it is not Rhynchocephalian, restores it with one temporal foramen and

one broad bar, and maintains that it is a little modified descendant of the ancestral lizard stock. Believing that the Lacertilia have been derived from such Synapsidan forms, he would separate them from the Rhynchocephalian and other Diapsidan orders. According, however, to Lortet's description and figures (21), one of which is reproduced here (fig. 3, E), the fifth metatarsal would appear to be of normal shape and size. If this interpretation is correct the evidence is distinctly against the view that Pleurosaurus is closely related to the ancestral lizard.

The Significance of the Heart and Aortic Arches in the Phylogeny of Reptiles.

Turning to the evidence to be derived from the structure of the heart and aortic vessels we shall find that it points unmistakably to the very same conclusion reached from a study of the hind foot, namely, that all the modern Reptilia have been derived from a single Sauropsidan branch, distinct from that which led to the Synapsidan Reptilia and the Mammalia.

It is well known that the heart of all reptiles (excepting the Crocodilia) is possessed of a single ventricle, that the cavity of this ventricle is incompletely subdivided by an incipient septum which is only completed in the Crocodiles, and that the four-chambered heart of the latter is essentially like that of a bird. In the possession of two completely separated ventricular chambers the heart of a bird resembles that of a mammal; and it is commonly stated that the two groups differ in that whereas in the former the aortic arch remains on the right side, in the mammal it is the left aortic arch which alone persists. But the difference is far more fundamental than such a statement implies.

The original aortic system, as shown by a comparison of the fish and the embryonic stages of the Tetrapods, consisted of six paired aortic arches. The first supplied the mandibular bar, the second the hyoid, and the remaining four the branchial bars. The last of these arches, the sixth of the original series, gives rise to the pulmonary artery. The heart itself consisted of a series of chambers: the posterior sinus venosus receiving the great veins; the atrium, which in air-breathing vertebrates becomes separated into two auricles; and a ventricle passing forward into a ventral aorta. This trunk becomes divided into a posterior contractile conus arteriosus, or bulbus cordis, and an anterior non-contractile truncus arteriosus, from which spring the aortic arches. The heart becomes twisted, so that the auricles come to lie dorsally and in front of the ventricle; but in the accompanying diagrams (fig. 4) of the heart and arches of an Amphibian (A), a Mammal (B), a Reptile (Lacertilian, Ophidian, Rhynchocephalian, or Chelonian) (C), and a

Crocodile (D), the hearts are represented as untwisted, so as to bring the chambers back into a single plane and facilitate comparison.

Now in the Amphibian a horizontal septum grows back, subdividing the lumen of the truncus into dorsal and ventral channels, and combines with one of the distal valves to form an oblique septum in the bulbus cordis, which septum directs most of the arterial blood into the ventral channel leading to the systemic and carotid arches, and most of the venous blood into a dorsal channel to the pulmonary arches. In the Amniota the valves are fully developed only in that narrow posterior region at the base of the bulbus, which becomes incorporated into the wall of the ventricle. The lumen of the truncus and bulbus becomes completely and spirally subdivided into two tubes, the pulmonary and the systemic or aortic. As shown by the work of Greil (15) and others, this is brought about by the completion of the horizontal septum with the help of the anterior valves of the bulbus. But whereas in the Mammalia the interventricular septum is so formed that the right (venous) ventricle leads only into the pulmonary artery, and the left (arterial) only into the aortic arch and carotids, in the Reptilia the interventricular septum tends to divide the chamber into a left cavity leading to the base of the right systemic arch, and a right cavity leading to the base not only of the pulmonary, but also of the left systemic arch. Thus, when the septum is completed, as in Crocodiles and Birds, the right ventricle opens into the pulmonary artery and left systemic arch, while the left ventricle opens into the right systemic arch. The two systemic arches cross over at their base, and the main arterial stream is always sent up the right arch, from which spring the carotids. The fundamental difference lies in the subdivision of the Sauropsidan bulbus down to its very root into two separate spirally twisted tubes, one crossing to the left and the other to the right, in such a way that the interventricular septum comes to pass between them. This line of specialisation inevitably leads in the long run to the Avian type, where the left systemic arch—already of little use in the Crocodile—disappears early in development. In the Mammal, on the contrary, the aortic trunk, separated from the pulmonary, never becomes subdivided at all, and the differentiation of the arteries has followed an independent and in many respects different course from the primitive bilaterally symmetrical pattern. The Theropsidan and the Sauropsidan types must have evolved from some more symmetrical primitive type, in which the ventricle and the aortic trunk were both single; and it does not seem possible for a heart which had once started, so to speak, to evolve along the Sauropsidan line to change its course and revert to the Theropsidan. The significance of this in determining the phylogeny of the Chelonia and the Lacertilia may now be pointed out.

Chelonia.—Opinions as to the affinities of the Chelonia have been widely divergent. Palæontology affords little or no evidence concerning the origin of this very isolated and specialised order. While some authors have pointed out resemblances to the Rhynchocephalia, Baur (1) and others have held that they are related to the Sauropsitygia. Jaekel (19) has derived them from

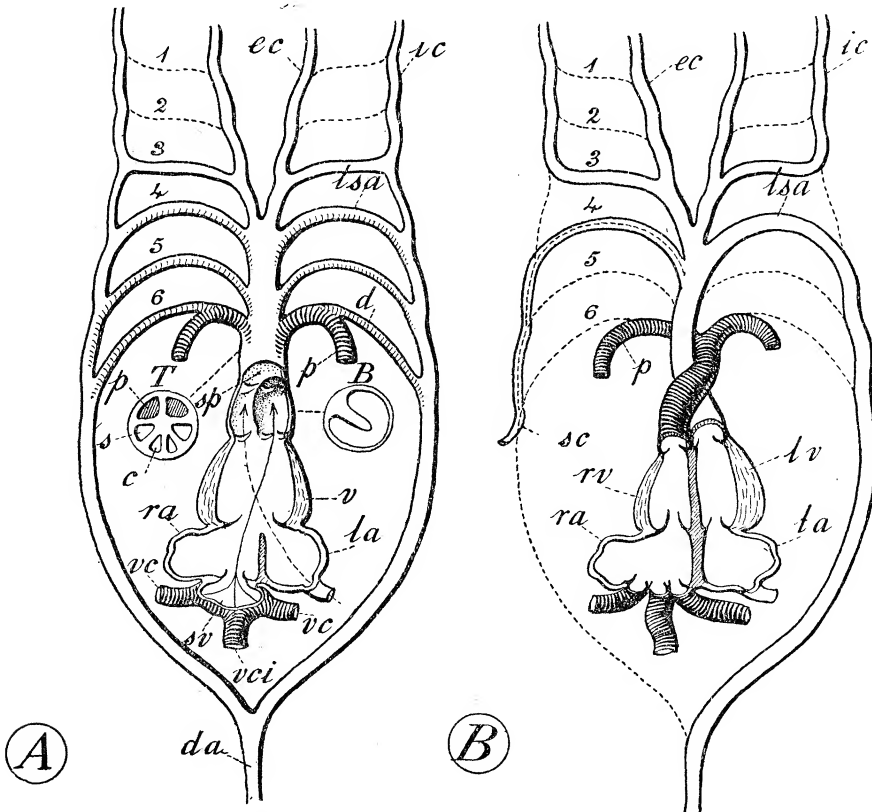
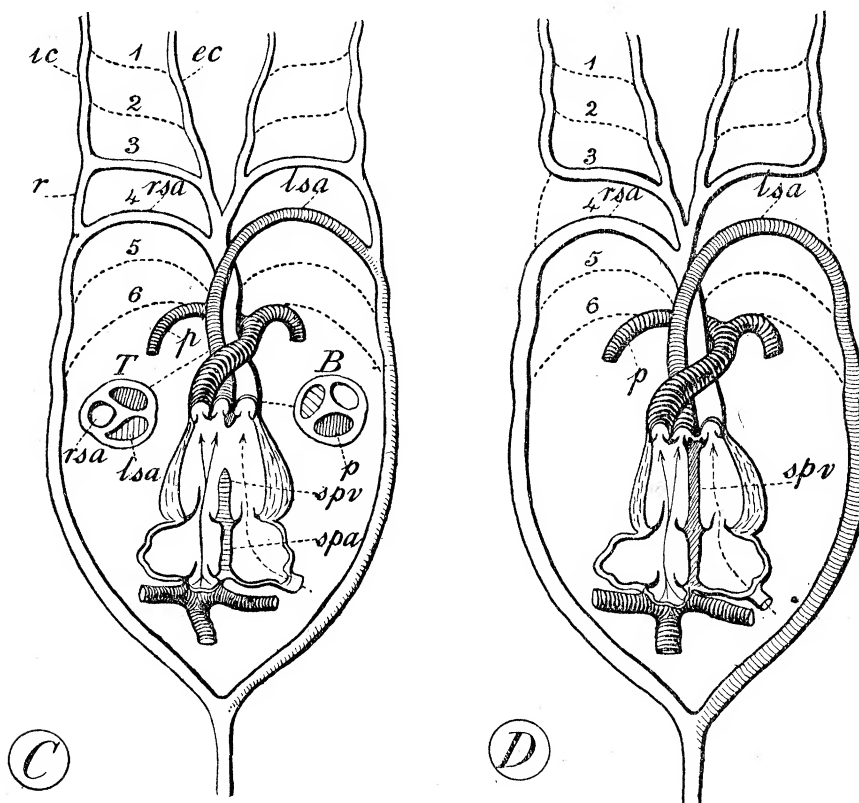


FIG. 4.—Diagrams of the Heart and Aortic Arches of an Amphibian (A), a Mammal (B), a Reptile (Chelonia, Lacertilia, Ophidia, Rhynchocephalia) (C), and a Crocodile (D); ventral view. The heart is represented as untwisted so as to bring the chambers into a single plane, with the sinus venosus behind and the ventricle in front. B, transverse section through region of the bulbous cordis; T, transverse section through the truncus arteriosus; d, ductus Botalli; ec, external carotid; ic, internal carotid; la, left auricle; lsa, left systemic arch; lv, left ventricle; p, pulmonary

Placodontia; but most recent writers prefer to derive them independently from some primitive Cotylosaurian ancestor, owing to the absence of true foramina in the temporal roof of the skull. Now the structure of the foot, provided with the characteristic hook-shaped metatarsal, and of the heart built on the Sauropsidan plan, clearly show that the Chelonia belong to the

Sauropsidan branch. There seems to be no escape from this conclusion; nevertheless, it does not solve the difficult problem of the true nature of the roofing of the skull. For it may still be held that the Chelonia branched off from the base of the Sauropsidan stem when the heart and metatarsal had become specialised but the roofing had not yet been pierced. On the whole,



artery; *r*, connecting region which remains open only in *Sphenodon* and certain *Lacertilia*; *ra*, right auricle; *rsa*, right systemic arch; *rv*, right ventricle; *sc*, subclavian; *spa*, interauricular septum; *spv*, interventricular septum; *sv*, sinus venosus; *v*, ventricle; *vc*, vena cava superior; *vci*, vena cava inferior. Arrows from the sinus venosus indicate the main stream of venous blood; arrows with a dotted line indicate the stream of arterial blood from the left auricle; 1-6, the original series of six aortic arches.

it seems more likely that the roofing of the skull has been secondarily restored, but the discovery of fossil intermediate forms alone can settle this question.

Lacertilia.—There is much difference of opinion as to the position of the order *Lacertilia* (including the *Pythonomorpha* and *Dolichosauria*). Some,

following Huxley (17), believe that the single temporal fossa of the lizard represents the upper fossa of *Sphenodon* limited below by the narrow upper temporal bar, while the lower temporal fossa is supposed to have become opened out in the dry Lacertilian skull, the lower bar being represented by a quadrato-jugal ligament. According to this view the Lacertilia are modified Diapsida. Many authors, however, including Baur (2), Williston (35), and Watson (33A), have held that the Lacertilia never had two fossæ, and that their skull is, in fact, built on the same plan as that of the Synapsidan Saurotheria (see p. 269). Here, again, an examination of the hind foot and heart (see pp. 264 and 270) shows us at once that the Lacertilia must belong to the Sauropsidan branch. The characteristic mesotarsal articulation and hook-shaped fifth metatarsal are typically developed, the aortic arches are separated and spirally crossed in the Sauropsidan manner. Palæontology can alone afford convincing proof as to the history of the skull, but the balance of evidence seems to be in favour of Huxley's view.

List of Some Genera Known to Have Normal Metatarsals.—Mesosauria—*Mesosaurus* (including *Stereosternum*). Nothosauria—*Lariosaurus* (Boulenger). Palæohatteria (Credner). Pelycosauria—*Varanosaurus* (Williston), *Dimetrodon*, *Ophiacodon* (Case), *Naosaurus* (Osborn), *Casea* (Williston), *Araucoscelis*? (Williston), *Pleurosaurus*? (Lortet).

List of Some Genera Known to Possess a Modified Fifth Metatarsal.—Chelonia—all living and extinct genera. Lacertilia—all living and extinct genera. Rhynchocephalia—*Sphenodon*, *Homœosaurus* (Lortet), *Saphœosaurus* (Gervais), *Rhynchosaurus* (Huxley), *Simœodosaurus* (Lemoine), *Champsosaurus* (Brown). Protorosaurus (H. v. Meyer). Pythonomorpha—*Tylosaurus* (Osborn), *Mosasaurus* (Dollo), Aetosauria—*Aetosaurus* (v. Huene). Parasuchia—*Rhytidodon* (McGregor). Crocodilia—all living and extinct genera. Also present, but in a reduced condition, in Dinosauria and Pterosauria.

Summary.

The group Reptilia represents not a true monophyletic class like the class Mammalia and the class Aves, but rather an assemblage or grade of Amniotes retaining a more primitive general structure. The Reptilia thus include a basal *Protosaurian* group of amphibian-like forms leading to a central point from which diverge two main branches—the *Sauropsidan* branch leading to the birds, and the *Theropsidan* branch leading to the mammals.

The modern classification of the reptiles, based chiefly on the structure of the skull, is in a very uncertain state. There is a great difference of

opinion as to the relationship of the various orders. Certain specialisations in the skeleton of the hind foot and in the structure of the heart and great vessels (in living forms) are of great importance in classification and deserve more weight than has hitherto been attributed to them.

The development of a hook-shaped fifth metatarsal and of a mesotarsal articulation, and the sub-division of the aortic trunk so as to form two systemic arches crossing at their base in such a way as to become separated by the interventricular septum, clearly distinguish the Sauropsidan from the Theropsidan line of evolution. The possession of these characters shows that all living Reptilia belong to the Sauropsidan group, while the structure of the foot enables us to determine the affinities of many incompletely known fossil genera, and to conclude that only certain extinct orders can belong to the Theropsidan branch.

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